

Three new species of *Parandrexia* (Coleoptera: Parandrexidae) from the Middle Jurassic Jiulongshan Formation of Inner Mongolia, China

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Abstract: Three well-preserved fossil species of *Parandrexia longicornis* Lu, Shih & Ren sp. nov., *P. agilis* Lu, Shih & Ren sp. nov. and *P. oblongis* Lu, Shih & Ren sp. nov., are described and illustrated from the late Middle Jurassic Jiulongshan Formation of Daohugou in Inner Mongolia Autonomous Region, China. These new species are distinguished from other described species of *Parandrexia* by body size, head dimension (ratio of length to width), pronotum shape, and antennal characters. Based on new morphological data, we emend the generic diagnosis. These findings support the sexual size dimorphism of parandrexids and suggest a gymnosperm sap feeding habit by *Parandrexia*.

Key words: fossil beetle; Daohugou; sexual size dimorphism; feeding habits; taxonomy; key

中国内蒙古九龙山组中侏罗世类天牛属三个新物种（鞘翅目：类天牛科）

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摘要：描述鉴定了来自中国内蒙古自治区道虎沟九龙山组中侏罗世的 3 个化石新种，长角类天牛 *Parandrexia longicornis* Lu, Shih & Ren sp. nov.，敏慧类天牛 *P. agilis* Lu, Shih & Ren sp. nov.和长圆类天牛 *P. oblongis* Lu, Shih & Ren sp. nov.。这 3 个新物种区别于类天牛其他物种的特征在于体型大小、头部形状（长宽比）、前胸背板形状和独特的触角。根据这些形态特征数据，本文修订了类天牛属属征。这些发现进一步证明了类天牛科具有雌雄二重性以及取食裸子植物汁液的食性。

关键词：甲虫化石；道虎沟；雌雄二重性；食性；分类；检索表

Introduction

Parandrexidae is a small extinct family of beetles (Coleoptera: Polyphaga: Cucujiformia: Cucujoidea) comprising two genera (Martynov 1926; Hong 1983; Kirejtshuk 1994; Soriano *et al.* 2006). Originally, *Parandrexia* was erected by Martynov as a genus of the subfamily Prioninae, which was assigned to the family Cerambycidae (Martynov 1926) in the superfamily of Chrysomeloidea. However, Kirejtshuk (1994) proposed a new family Parandrexidae and assigned it to the infra-order Cucujiformia (Coleoptera: Polyphaga). In 2006, Soriano accepted this systematic placement and established a new genus in this family and put this family in the superfamily Cucujoidea (Soriano 2006). In this article, we follow

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this systematic classification.

Previously, only four fossil species in the *Parandrexia* Martynov, 1926 had been described: *P. parvula* Martynov, 1926; *P.* (= *Parandrexia* Hong, 1983) *beipiaoensis* Hong, 1983; *P. rotundicollis* Kirejtshuk, 1994 and *P. subtilis* Kirejtshuk, 1994. *Martynopsis* Soriano, 2006 held only one species, *M. laticollis* Soriano, 2006 from the Lower Cretaceous of Las Hoyas in Barrenmian of Spain (Soriano 2006).

Recently, five well-preserved fossil parandrexid specimens were collected from the late Middle Jurassic Jiulongshan Formation at Daohugou Village, Ningcheng County, Inner Mongolia, China. Based on their unique morphological characters, we describe three new species and assign them to the *Parandrexia*. In addition, we identify and assign a female specimen to the previously described *P. parvula*.

The age of Jiulongshan Formation is late Middle Jurassic, about 165 Ma (Chen *et al.* 2004; Gao & Ren 2006; Ren *et al.* 2010; Wang *et al.* 2013), corresponding to the Callovian-Bathonian boundary from the most recent geochronologic time scale (Ogg *et al.* 2008). The Daohugou fossil site has yielded rich fossil insects (Ren *et al.* 2009; Gao *et al.* 2012, 2013; Wang *et al.* 2010, 2012), including many beetles (Liu *et al.* 2007; Tan & Ren 2009; Ponomarenko & Ren 2010; Bai *et al.* 2012; Tan *et al.* 2012). Reconstruction of the paleoenvironment shows that it was a volcanic region with mountains, streams and lakes and a humid and warm-temperate climate (Ren *et al.* 2002; Tan & Ren 2002; Gao & Ren 2006).

Material and methods

All fossil specimens are housed in the Key Lab of Insect Evolution & Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong REN, Curator). The specimens were examined dry or under alcohol using a DFC500 Leica dissecting microscope, illustrated with the aid of a drawing tube attachment and photographs taken with a Nikon Digital Camera DXM1200C. The figures were drawn by Adobe Photoshop CS 5 graphic software. The morphological terminology used here follows Newton *et al.* (2001), and the Parandrexidae taxonomic system is adopted from Lorenz (2005).

Body length was measured along the midline from the anterior margin of frons to apex of elytra, and width was measured across the broadest part of elytra. The length of pronotum was measured along the midline; the width was measured across the broadest part of pronotum. Abdomen length was measured along the midline and the width was measured across the broadest part. (Ren *et al.* 2014; Zhou & Chen 2014).

Systematic paleontology

Class Insecta Linnaeus, 1758

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Infraorder Cucujiformia Lameere, 1938

Superfamily Cucujoidea Latreille, 1802

Family Parandrexidae Kirejtshuk, 1994

Genus *Parandrexia* Martynov, 1926

Type species. *Parandrexia parvula* Martynov, 1926

Emended Diagnosis. Body slender or oblong. Antenna filiform, 11–12 segmented. Scape forming a clavate structure. Mandibles very long and narrow in males (much shorter than head in females). Maxillary palp 3–4 segmented, thin and long. Mesothorax somewhat short and metathorax longer than mesothorax. Scutellum triangular. Prosternal lobe not projecting to mesocoxae. Femur fusiform but not strong Tibia much thinner than femur, as long as femur and slightly widening towards apex. Tarsus 4-segmented, short and thin, the distal tarsomere longer than others, claws simple. Females having approximately the same outlines as males, but with larger body size, shorter antennae and shorter mandibles.

Remarks. We assign these three new species to *Parandrexia* based on the following features: small and elongate body; large head with strong mandibles and long palps; long filiform antennae; scape forming a clavate structure; and elytra covered by apparent punctuation and striae.

Taxonomy

1. *Parandrexia longicornis* Lu, Shih & Ren sp. nov. (Fig. 1)

Holotype. CNU-COL-NN-2010502P/C (♂). The male is well preserved in dorsal and ventral views. All tarsi and some structures of mesothorax are not preserved.

Description. A comparatively large parandrexid. Body elongated. Head large and transverse. Compound eyes relatively large, located at the widest part of head. Mentum wide, almost reaching edges of eyes. Mandibles long, narrow and narrowing from base to apex, without sharp hook. Length of mandibles shorter than head and pronotum combined. Maxillary palp slender, 3-segmented. Labium trapeziform. Antenna 11-segmented, almost as long as body excluding mandibles, located just between mandibles and eyes. Scape clavate and pedicel half size of the scape. The other 9 antennomeres slender and of the same length. A distinct protuberance at the terminal of last antennomere.

Pronotum transverse, somewhat convex, widest at anterior margin, narrowing posteriorly; as wide as head and 3/5 as long as the head. Anterior margin obviously arching with two obtuse corners, and posterior margin concave without distinct corner. The prosternal lobe clear and not projecting beyond procoxae. Scutellum triangular. Prothorax and mesothorax relatively short and metathorax longest. Mesepisternum and mesepimeron visible, small and square. Metepisternum and metepimeron rectangular, close to mesocoxal cavity. Posterior margin of metasternum horizontal.

Legs slender, not strong. Femur fusiform, tibia more slender than femur, and tarsus not preserved. Procoxae transverse rectangular and open. Mesocoxae oval and closed. Metacoxae transverse and triangular. Abdomen with 5 visible segments. All of abdominal segments approximately of equal length.

Elytra anterior margin subtruncate and shoulder corner distinct. Elytra covered by even punctuation and apparently dense striae. Abdomen completely covered by elytra.

Dimensions (in mm). Holotype. Body excluding mandibles length 13.5, width 3.8. Mandible length 3.9. Antenna length 12.3. Head length 2.6, width 3.4. Elytra length 5.9, width 4.0. Pronotum length 1.5, width 3.5.

Diagnosis. Antennae equal to body length. Mandibles ending with obtuse teeth. Scape extraordinary thick. Maxillary palp 3-segmented. Eyes large, oblong. Pronotum bowl-shaped.

Elytra covered with dense striae and scattered punctation.

Etymology. The specific epithet is from the Latin *longus* (long) and Latin *cornis* (antenna).

Remarks. *Parandrexia longicornis* sp. nov. differs from *Parandrexia agilis* sp. nov. and *Parandrexia oblongis* sp. nov. by the following features: (1) relatively large body; (2) antennae equal to body length; (3) maxillary palp 3-segmented; (4) pronotum bowl-shaped.

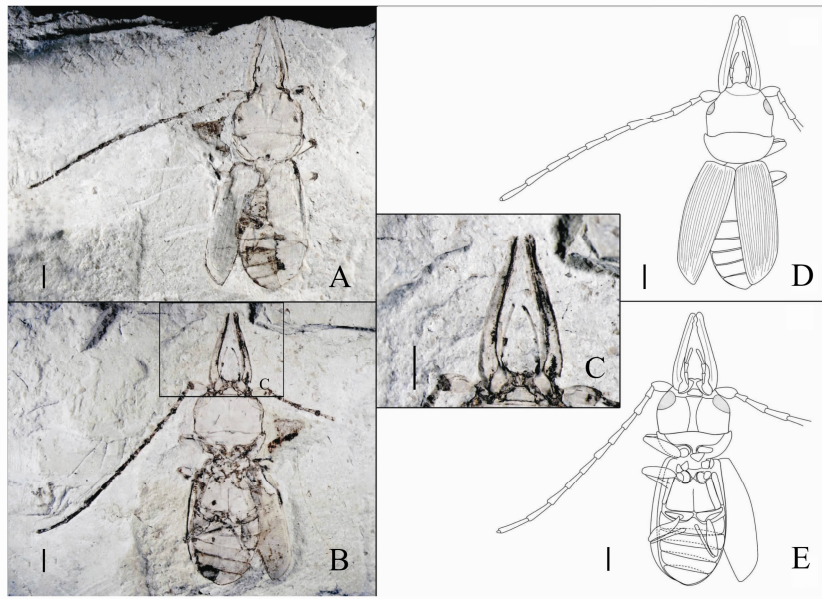


Figure 1. *Parandrexia longicornis* Lu, Shih & Ren sp. nov. Holotype, CNU-COL-NN-2010502P/C (♂). A. Photograph of part, dorsal view; B. Photograph of counterpart, ventral view; C. Photograph of mouthparts, ventral view; D and E. Line drawings of part and counterpart. Scale bars = 1 mm.

2. *Parandrexia agilis* Lu, Shih & Ren sp. nov. (Figs. 2, 3)

Holotype. CNU-COL-NN-2010501P/C (♂). Paratype. CNU-COL-NN-2013001 (♂). The holotype is well preserved in dorsal and ventral views. Most of tarsi and some structures of mesothorax are not preserved. The paratype is well preserved in dorsal view. One hind femur and two hind coxae are visible.

Description. (Holotype, Fig. 2) An elongated parandrexid of moderate size. Head large, transverse, and nearly twice as long as pronotum, almost equal to pronotum in width. Compound eyes round, not large, located at the widest part of the head. Mentum wide, almost reaching edges of eyes. Mandibles narrow and longer than head and pronotum combined, narrowing from base toward apex. Maxillary palp slender, 4-segmented. Labium trapeziform. Antenna filiform, 11-segmented, shorter than body (excluding mandibles) and head combined, located just between mandibles and eyes. Scape clavate, and pedicel half the size of the scape. The other 9 antennomeres slender and the same length.

Pronotum approximately rectangular, transverse, somewhat convex, widest at anterior margin, slightly narrowing posteriorly and without distinct corner. Prosternal lobe clear and extending beyond procoxae. Scutellum triangular. Prothorax shortest, mesothorax and

metathorax of equal length. Legs not very strong. Femur long, extending outward from the body. Procoxae transverse, rectangular and open. Mesocoxae oval and closed. Metacoxae transverse and oblong. Femur fusiform, tibia more slender than femur, widening from base toward apex. Tarsi 4-segmented.

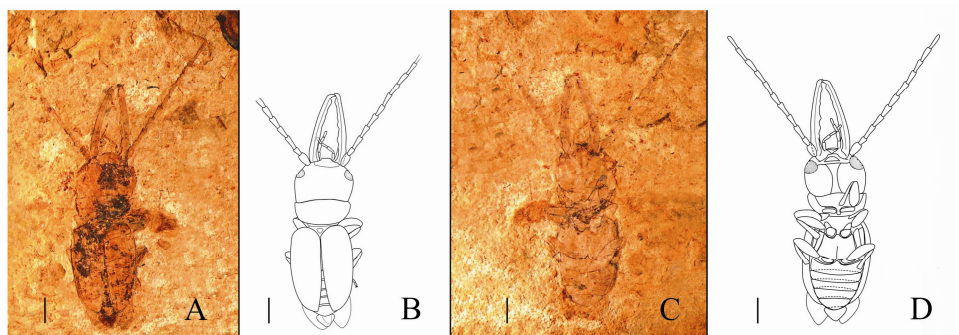


Figure 2. *P. agilis* Lu, Shih & Ren sp. nov. Holotype, CNU-COL-NN-2010501P/C (♂). A. Photograph of part, dorsal view; C. Photograph of counterpart, ventral view; B and D. Line drawings of part and counterpart. Scale bars = 1 mm.

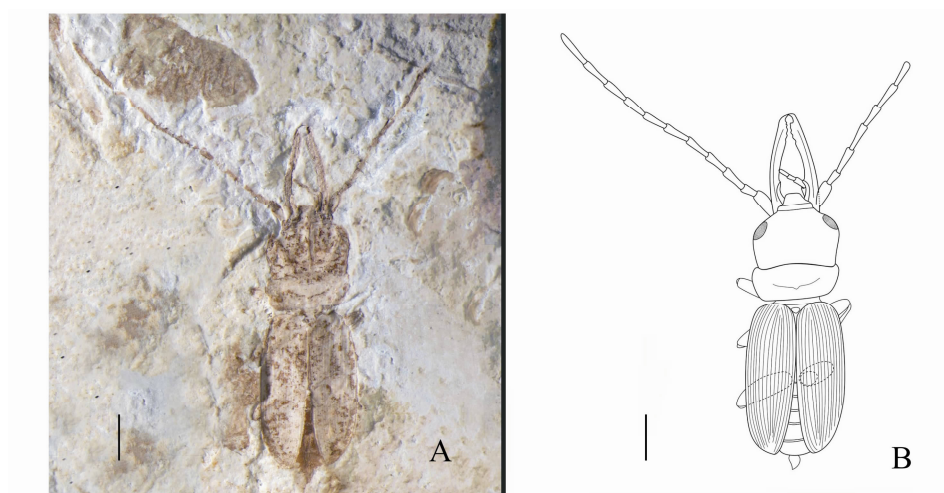


Figure 3. *P. agilis* Lu, Shih & Ren sp. nov. Paratype, CNU-COL-NN-2013001 (♂). A. Photograph, dorsal view; B. Line drawing. Scale bars = 1 mm.

Elytra rounded at base and as wide as the posterior margin of pronotum, and with apparent punctuation. The length of elytra 1.5 times as long as wide.

Abdomen not completely covered by elytra, part of the last sterna and genitalia exposed. Hind wing partially preserved but not discernible. Abdomen with 5 visible segments. All sterna of approximately equal length.

(Paratype, Fig. 3) With exactly the same characters as the holotype. Labrum prominent. Clypeus discernible. Elytra with apparently dense striae on the surface. Hind coxae transverse

and oblong.

Dimensions (in mm). Holotype. Body length excluding mandibles 10.9, width 2.9. Mandibles length 3.7. Antenna length 6.9. Head length 2.2, width 2.8. Elytra length 4.7, width 2.9. Pronotum length 1.2, width 2.7.

Paratype. Body length excluding mandibles 8.3, width 2.4. Mandibles length 2.2. Antenna length 6.5, elytra length 3.6, width 2.4. Head length 1.6, width 2.0. Pronotum length 0.8, width 2.0.

Diagnosis. Mandible longer than head and pronotum combined, hooked at the apex, with evenly contoured inner edge and a sharp tooth at the base. Maxillary palp 4-segmented and slender antennae shorter than body excluding mandibles and head. Pronotum approximately rectangular, transverse. Eyes round. Elytra covered with dense striae. Hind coxae transverse oblong. Two claws, simple.

Etymology. The specific epithet is from the Latin *agilis*, meaning agile.

Remarks. *Parandrexia agilis* sp. nov. differs from *Parandrexia longicornis* sp. nov. and *Parandrexia oblongis* sp. nov. by the following characteristics: (1) mandible hooked at the apex; (2) maxillary palp 4-segmented; (3) antennae shorter than body excluding mandibles and head; (4) pronotum approximately rectangular, transverse.

3. *Parandrexia oblongis* Lu, Shih & Ren sp. nov. (Fig. 4)

Holotype. CNU-COL-NN-2013002P/C (♂). Well preserved in dorsal and ventral views. All tarsi, three legs, and some structures of pro- and mesothorax are not preserved.

Description. A relatively small and oblong parandrexid. Head and pronotum strongly transverse. Mandibles very long and strong, twice as long as head, and longer than head and pronotum combined, with distinct contoured inner edge. Labrum forming a bend towards trapezoid labium. Five slender antennomeres preserved, scape very long and thick and pedicel half the size of the scape. Compound eyes small in dorsal view but very large in ventral view. Mentum transverse. Frons-clypeus suture obvious. Head length twice head width. Pronotum somewhat shorter than head but equal in width.

Pronotum very transverse, anterior margin slightly curved and posterior margin straight, posterior corner concave. Pronotum width more than twice pronotum length. Prothorax and metathorax slightly longer than mesothorax. Procoxae not preserved. Prosternal lobe exposed. Midcoxae oval and hindcoxae very transverse, wide. Legs extending out of body line. Femora fusiform and thick, tibia thin, straight and widening from base toward apex. One segment of metatarsus visible.

Each of four sterna of equal length, but the fifth is longer than the others. Elytra covered with marked punctation and eight apparent striae. Elytra length 1.3 times as long as the width of both elytra combined. A well-developed epipleura forming a distinct bend in plane of elytra.

Dimensions (in mm). Body excluding mandibles length 6.9, width 2.8. Mandibles length 2.9. Head length 1.6, width 2.8. Elytra length 4.4, width 2.8. Pronotum length 1.1, width 2.8.

Diagnosis. Body small and oblong. Head and pronotum very transverse. Mandible twice as long as head, longer than head and pronotum combined, without hook at the apex. Compounded eye larger than labium. Elytra covered with eight striae. Legs strong. Middle coxae oval and hind coxae oblong.

Etymology. Specific epithet is from the Latin *oblongus*, meaning long and oval.

Remarks. *Parandrexia oblongis* sp. nov. differs from *Parandrexia longicornis* sp. nov. and *Parandrexia agilis* sp. nov. by the following features: (1) body small and oblong; (2) head and pronotum very transverse; (3) mandible twice as long as head, without hook at the apex; (4) elytra covered with eight striae.

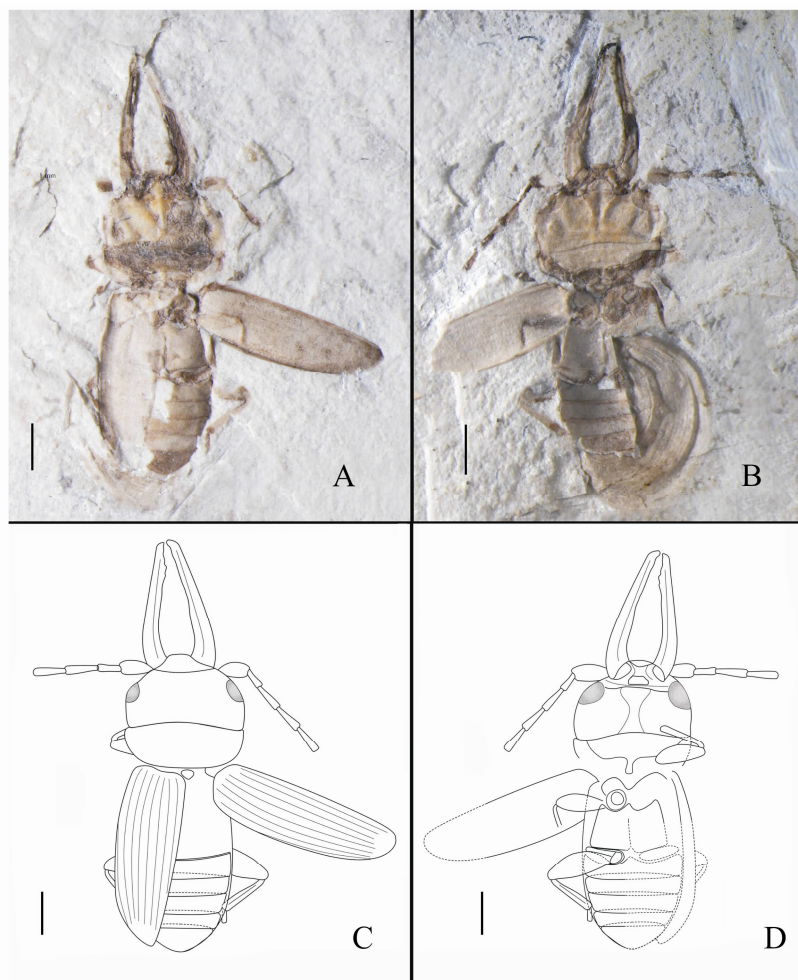


Figure 4. *P. oblongis* Lu, Shih & Ren sp. nov. Holotype, CNU-COL-NN-2013002P/C (♂). A. Photograph of part, dorsal view; B. Photograph of counterpart, ventral view; C and D. Line drawings of part and counterpart. Scale bars = 1 mm.

4. *Parandrexia parvula* Martynov, 1926 (Fig. 5)

Additional material. CNU-COL-NN-2013003 (♀). Well preserved in ventral view, most of tarsi and some structures of pro- and mesothorax are not preserved.

Description. Body small and elongated, bearing the same outline as in the male, but with shorter mandibles and shorter antennae.

Head transverse square. Mandibles sickle-shaped, relatively broad, but shorter than head. Maxillary rectangular. Labrum forming a bend towards labium and labium trapezoidal. Mentum wide, almost reaching edges of eyes. Compound eyes larger than labium. Gena

transverse. Antennae shorter than body excluding head and mandibles.

Prothorax as long as metathorax. Mesothorax slightly shorter. Abdomen somewhat longer than mesothorax and metathorax combined. Each sterna of nearly the same length.

Procoxae not discernible. Prosternal lobe exposed. Midcoxae oval, closed with a gap between them. Metepimeron rectangular and as long as metasternum. Posterior margin of metasternum straight. Hind coxae strongly transverse. Femur fusiform, not strong, slightly extending outside the body, with widening apex. Tibia thin and widening toward apex. Four segments of tarsus visible, the fourth one longest and claws simple.

Abdomen not completely covered by elytra. Elytra 1.5 times as long as the width of two elytra combined.

Dimensions (in mm). Body excluding mandibles length 6.6, width 2.5. Mandible length 0.9. Antenna length 4.6. Head length 1.5, width 2.0. Pronotum length 1.0, width 2.2. Elytra length 3.9, width 2.5.

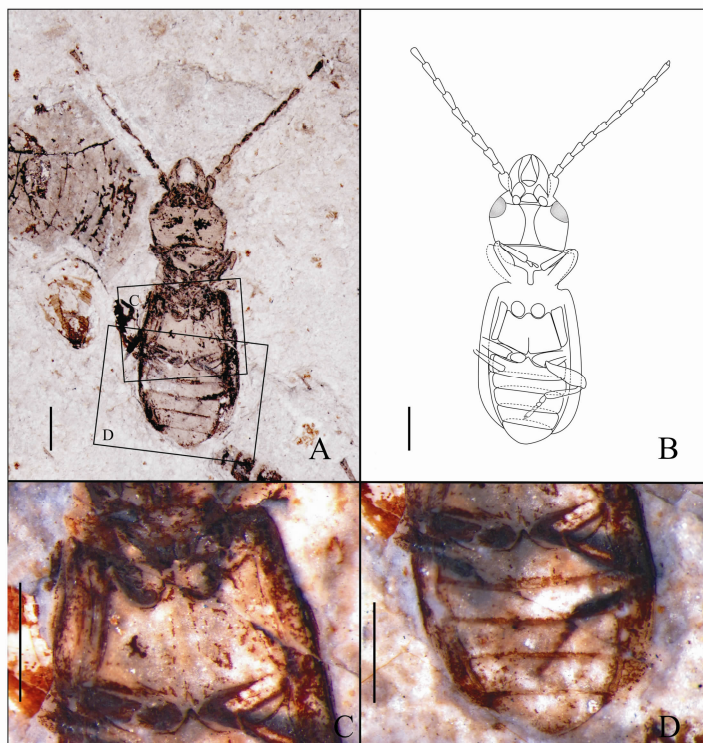


Figure 5. *P. parvula* CNU-COL-NN-2013003 (♀). A. Photograph, ventral view; B. Line drawing; C. Photograph of meso- and metathorax under alcohol; D. Photograph of abdomen under alcohol. Scale bars = 1 mm.

Key to all species (only male) of *Parandrexia* Martynov, 1926

1. Body long and narrow; the ratio of body length (excluding mandibles) to width is greater than 33
- . Body somewhat oval; the ratio of body length (excluding mandibles) to width is less than 32
2. Mandibles short, 3/5 as long as head; antennomeres thick; pronotum sharply narrowing posteriorly, without pronounced posterior corners*P. rotundicollis* Kirejtshuk
- . Mandibles very long, 1.5 times of head; antennomeres slender; anterior margin of pronotum as wide as

- posterior margin; posterior corners pronounced6
3. Head shorter than pronotum; each elytra of length almost twice as wide as two elytra combined; pronotum trapezoidal *P. subtilis* Kirejtshuk
- Head long, length of head more than 1.5 times of pronotum; length of elytra 1.5 times as wide as both elytra combined4
4. Body length 18 mm; antennae 12 segments; pro- and mesocoxae oval *P. beipiaoensis* Hong, 1983
- Body shorter than 15 mm; antennae 11 segments; procoxae transversely rectangular and mesocoxae oval5
5. Antennae almost as long as body excluding mandibles; maxillary palp 3-segmented; apex of mandibles rounded and having obtuse teeth but no sharp teeth at the base *P. longicornis* sp. nov.
- Antennae shorter than body excluding head and mandibles; maxillary palp 4-segmented; apex of mandibles hooked, sharp and with a sharp tooth at the base *P. agilis* sp. nov.
6. Mandibles hooked at the apex; metathorax longer than prothorax; pronotum widening strongly from base forward *P. parvula* Martynov
- Mandibles strong and obtuse; metathorax is almost as long as prothorax; pronotum strongly transverse and widening slightly forward *P. oblongis* sp. nov.

Table 1. Statistical dimension data of females and males in *P. parvular* (in mm)

Specimen number	Body length (Excluding mandibles)		Mandible length		Antenna length	
	male	female	male	female	male	female
Martynov 1926. Fig. 12	5.5		1.9		5.7	
PIN No. 2384/701	5.5		1.2		5.8	
PIN No. 2997/438	6.0		3.1		7.0	
PIN No. 2997/4507	6.6					
Martynov 1926. Fig. 10		4.5		0.6		3.2
PIN No. 965/34		5.7		0.6		>4
PIN No. 2066/2878		6.4		0.9		4.8
CNU-COL-NN-2013003		6.6		0.9		4.6
PIN No. 2997/440		6.7		0.7		
PIN No. 1789/48		7.0		0.7		5.0
PIN No. 2452/248		7.2		1.1		4.7
PIN No. 965/31		7.3		1.0		5.3
Average	5.9	6.4	2.1	0.9	6.2	4.6
Variance	0.2	0.8	0.6	0.04	0.4	0.4

Discussion

Sexual Size Dimorphism and Copulation

Sexual size dimorphism (SSD) is a widespread phenomenon in all animal taxa and has been studied for many years (Darwin 1871; Shine 1989; Badyaev 2002; Blanckenhorn 2005). Female-biased SSD is common among insects (Hochkirch & Gröning 2008; Shine 1979). For example, females in many species of stick insects (Order Phasmatodea) have a significantly larger body size than males (Wang & Yang 2005). On the other hand, male-biased SSD has been reported in beetles (Stillwell *et al.* 2010). Males of some beetles, e.g. Lucanidae, have elongated mandibles on the head for fighting and competing with other males, but female

individuals don't have these specialized structures. The body sizes of these male beetles are larger than those of females (Tatsuta *et al.* 2001).

As reported, species of the *Parandrexis* have different sizes of specific organs among males and females. Males of *Parandrexis* species have long and robust mandibles and long antennae. But females of the same species have shorter and less robust structures (Martynov 1926; Kirejtshuk 1994). We summarize all measurements of reported specimens of the *Parandrexis parvula* Martynov, 1926 in Table 1. For males, the average body length (excluding mandibles), mandible length, and antennae length are 5.9 mm, 2.1 mm, and 6.2 mm respectively. The variances are 0.2 mm, 0.6 mm, and 0.4 mm respectively. For females, the average body length (excluding mandibles), mandible length, and antennae length are 6.4 mm, 0.9 mm, and 4.6 mm respectively. The variances are 0.8 mm, 0.04 mm, and 0.4 mm respectively. The data show that males of *P. parvula* have a body size generally smaller than that of females, but males have longer and more robust mandibles, and longer antennae.

Feeding Habits

The most prominent feature of this genus is the long mandibles. Kirejtshuk (1994) stated that the elongation of the mandibles without intensification of their incisorial function and very long maxillary and labial palps suggest they were sap-feeding beetles on the surface of the strobiles of Mesozoic gymnosperm plants. As for males of *P. parvula*, the larger mandibles might have provided a tool for the males to defend their feeding sites and to gain access to females, as in the Cerambycidae (Goldsmith 1987). The sharp mandibles of females might have been used for digging tunnels in the host plant and ovipositing in the tunnels (Chiappini & Aldini 2011).

Conclusions

Three well-preserved fossil species of *Parandrexis longicornis* sp. nov., *P. agilis* sp. nov., and *P. oblongis* sp. nov. are described from the late Middle Jurassic Jiulongshan Formation of Daohugou in Inner Mongolia, China. These new species highlight the diversity of Parandrexidae in its ecosystem. Based on new morphological data, we emend the generic diagnosis and set up a key to all male species of *Parandrexis*. In addition, these findings support the sexual size dimorphism for parandrexids and suggest a gymnosperm sap feeding habit by *Parandrexis*.

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